

INDUCIBLE RESPONSE OF *PSEUDOMYRMEX SPINICOLA* TO HERBIVORY ON *ACACIA COLLINSII*

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Abstract: The mutualistic relationship between *Pseudomyrmex spinicola* and *Acacia collinsii* is based on ants providing a defense response for the tree in exchange for tree-provided shelter and food. We hypothesized that this ant defense is induced by leaf damage and/or physical disturbance caused by a foraging herbivore. We tested for an inducible response to herbivory by cutting leaflets (simulated herbivory) and by tapping branches (simulated herbivore presence) on host *Acacias*. We found significantly greater ant response to both leaf damage and physical presence compared to controls: there was a 3-fold increase in ant response to leaf damage and a 5-fold increase in response to physical presence. Our results therefore show that *P. spinicola* does provide an inducible defense against herbivory for *A. collinsii*. The cues used by the ants to respond to these disturbances, however, require further study.

Key Words: ant-acacia, inducible defense, mutualism, symbiosis

INTRODUCTION

Plants have developed a variety of different defenses in response to herbivory. *Acacia collinsii* in South and Central America has a mutualistic relationship with *Pseudomyrmex spinicola* and other ant species. The ants protect trees from herbivory and competing plants in exchange for food in extra-floral nectaries and protein-rich Beltian bodies (Janzen 1983). These acacia trees have no documented chemical defenses. Instead, their mutualistic ants may function in a way analogous to chemical compounds in other plants. Research has shown that such chemical defenses can be induced by the presence and/or damage caused by herbivores (Ricklefs 1990). We therefore hypothesized that acacia ants may respond to stimuli corresponding to an herbivore attack, i.e., show an inducible response. We predicted that ants would respond to cues released by the host tree when damaged by a foraging herbivore, and/or to the physical presence of an herbivore on the plant.

METHODS

The study was conducted on a windy,

overcast morning in Palo Verde National Park, Costa Rica, ≈ 1 km E of the OTS field station, and 100 - 200 m south of the road. Twelve well-foliated *A. collinsii* trees, 1 - 4 m tall, were selected haphazardly for each experiment.

Leaf cutting experiment. To investigate the response to leaf damage (simulated herbivory), we haphazardly selected an acacia with healthy-looking foliage in the central range of an eye-level branch on each of the 12 trees. Using a pair of scissors, we snipped treatment leaves once through half of the leaflets on one side of the leaf and once across the top of the rachis. A leaf with similar attributes on the opposite side of each tree, touched in the same manner, served as a control. Instantaneous counts of the ants present on the cut leaf and the control leaf were taken at 10 s intervals for 30 s before and 60 s after cutting and then at 30 s intervals for the next 5 min. To control for differences in baseline ant activity among sampled trees, the average of pre-treatment ant abundance for each tree was subtracted from post-treatment ant abundance on that tree at each sample time. These relative ant abundances were analyzed in a repeated measures analysis of variance.



Mechanical disturbance experiment. To investigate the response to mechanical disturbance (simulated herbivore presence), experimental and control branches were selected in the same manner as above on a different set of 12 *Acacia* trees. The treatment branch was disturbed at the central point by rapid tapping with a pen for 10 s while the control branch was left undisturbed. The number of ants crossing an imaginary control line on each branch was counted during 10 s intervals for 30 s before, 10 s during, and 30 s after the disturbance. We controlled for differences in baseline ant activity in the same manner as above, and used these relative ant abundances in a repeated measures analysis of variance.

RESULTS

Leaf cutting experiment. Post-treatment *P. spinicola* abundance was significantly greater on damaged branches than on control branches ($F_{1,22} = 4.91$, $p = 0.037$). Mean ant

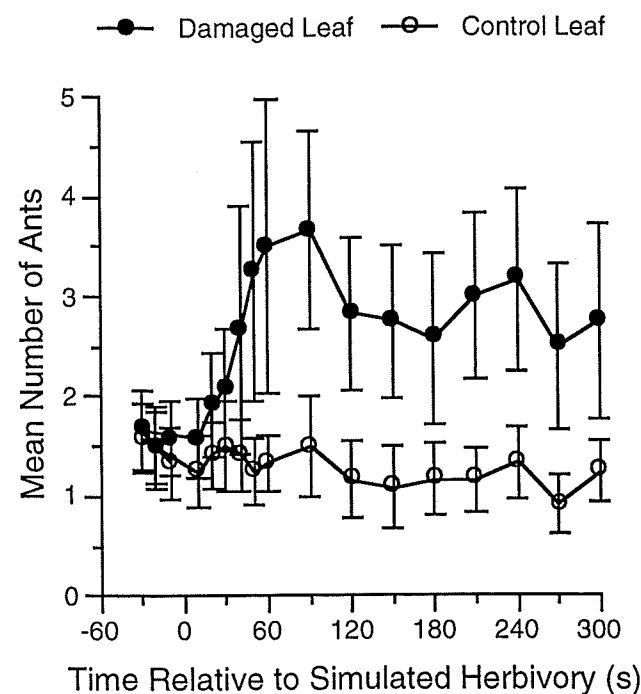


Fig. 1. Mean number (\pm SE) of *Pseudomyrmex spinicola* on damaged and control leaves from 30 s before to 300 s after simulated herbivory ($n = 12$ for both treatment and control).

abundance increased dramatically after leaf disturbance, followed by a relatively stable defense response through 300 s of observation (Fig. 1).

Mechanical disturbance experiment. The mean number of *P. spinicola* crossing the central branch point was significantly greater in disturbance than control treatments ($F_{1,22} = 21.25$, $p < 0.001$). Mean number of ants crossing the point of disturbance rose sharply during the disturbance interval and remained higher than the control for all intervals after

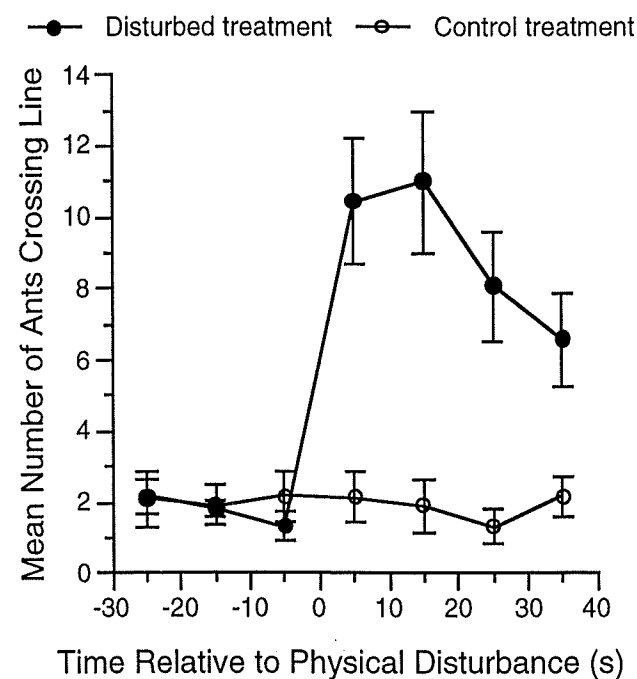


Fig. 2. Mean number (\pm SE) of *Pseudomyrmex spinicola* ants crossing an imaginary line on *Acacia collinsii* branches during 10 s intervals ($n = 12$ for both treatment and control). Means are shown at the midpoint of each time interval. Disturbed treatment branches were tapped

DISCUSSION

Both leaf damage (simulated herbivory) and physical disturbance (simulated herbivore presence) elicited a significant increase in number of ants present at the area of disturbance. These results show that ant defense is induced by both the physical damage

and mechanical disturbance of an herbivore. Although the mechanisms underlying these responses were not investigated, cues used by ants to detect these disturbances may involve detection of a volatile compound released by the damaged leaves (damage response) and vibrations caused by an herbivorous insect landing on the tree (mechanical response).

Mechanical disturbance recruited a higher number of ants to the site of disturbance than did leaf damage. We present four possible explanations for this difference. First, the magnitudes of our simulated disturbance events may have been unequal. We were unable to control for differences in the absolute level of disturbance between tapping and leaf damage. Second, ant response may be inversely proportional to their distance from the disturbance. Tapping a branch on which ant-inhabited thorns are located, for example, may present a more immediate threat to the colonies than damage to remote leaves. Third, if damaged leaves release a volatile chemical to which the ants respond, such volatiles would be easily diluted with distance. It is thus possible that such cues from damaged leaves would never be sensed by ants in more distant thorns. Fourth, time lags may be associated with the dispersal of the alarm pheromones used by ants to communicate with each other (Broughton et al. 1994). The duration of our experiment (300 s) may not have been long enough to allow detection of such potential time lags.

The inducible defense response of *P. spinicola* appears to be an energy efficient solution for both ant and acacia. Rather than patrol the tree's branches constantly, ants only need to invest energy in defense when it is essential. The acacias, on the other hand, spend a constant amount of energy in providing ants with nectaries and thorn shelter, but do not need to invest heavily in the production of costly defense compounds. Instead, they depend on ants for immediate defense.

The induction responses of *P. spinicola* shown in our experiments reflect the ants' attempt to defend the host tree. By decreasing herbivory, ants help to increase their host tree's fitness and therefore its ability to produce nectar and Beltian bodies that in turn support the ant colony. At the same time, better provisioned ants are better able to protect acacias from herbivory and competition from other plants.

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